Great Basin Naturalist 50(1), 1990, pp. 21–31

FORM AND DISPERSION OF MIMA MOUNDS IN RELATION TO SLOPE STEEPNESS AND ASPECT ON THE COLUMBIA PLATEAU

George W. Cox[1]

ABSTRACT.—Patterned ground consisting of Mima-type earth mounds and associated sorted stone circles and nets is widespread on the Columbia Plateau of western North America. Studies of the geometric relationships of mounds and stone nets to slope aspect and steepness were carried out at the Lawrence Memorial Grassland Preserve, north central Oregon, in June 1987. Mound and moundfield characteristics were sampled on randomly chosen 1-ha plots on slopes of different aspect and steepness. Mounds were largest, most circular and symmetrical in form, and most fully encircled by beds of size-sorted stones on level sites. On slopes of increasing steepness, mounds decreased in size, showed increasing asymmetry and downslope elongation, and became connected into lines oriented up- and downslope. Encircling stone beds became more weakly developed or disappeared on upslope and downslope sides of the mounds, and the lateral beds developed downslope extensions that eventually merged with those of adjacent upslope and downslope mounds. These patterns are interpreted as reflecting changes in the manner of soil translocation by northern pocket gophers, *Thomomys talpoides*, due to their responses to tunneling on slopes and to the modification of the flow of water across the slope because of the presence of mounds.

Mima-type earth mounds are a characteristic feature of grasslands with shallow soils or poor drainage in western North America (Cox 1984). These mounds, containing stones up to about 50 mm in diameter, commonly range up to 2 m in height, 20 m in diameter, and 50 ha^{-1} in density. Recent investigations at several locations have supported the hypothesis that Mima-type mounds are formed over long periods of time by the centripetal translocation of soil toward centers of activity of geomyid pocket gophers. These centers, located initially in the deepest, best drained sites available, are gradually transformed into mounds by soil translocation (Cox 1984, Cox and Allen 1987b, Cox and Gakahu 1987, Cox et al. 1987).

Mima mounds are an extensive and prominent feature of the shrub steppe of the Columbia Plateau in eastern Washington, northern Oregon, and southwestern Idaho, USA. Here the mounds are frequently encircled by beds of sorted stones, and intermound flats often exhibit polygonal networks of sorted stone beds (Waters and Flagler 1929, Kaatz 1959, Malde 1961, 1964, Fosberg 1965). These features, formerly interpreted as periglacial features, have also been interpreted as a result of soil translocation by pocket gophers (Cox and Allen 1987a).

Our previous studies of Mima mounds and sorted stone beds have been conducted on level areas where mounds are circular in form and regular in spacing. Observations by previous workers (cited above) and patterns evident on aerial photographs indicate that mound form and moundfield geometry are modified considerably on slopes. The objective of this study was to define variation in mound form and moundfield geometry with slope aspect and steepness, and to determine if the activities of pocket gophers can account for the variation.

METHODS

Studies were conducted at the Lawrence Memorial Grassland Preserve (LMGP) and on adjacent ranch land of the Priday Brothers Corporation, southern Wasco County, Oregon (44°57′N, 120°48′W), 1–11 June 1987. This was the site of previous studies of the structure of mounds and associated beds of sorted stones (Cox and Allen 1987a, Cox et al. 1987). The LMGP, a registered national landmark owned by the Nature Conservancy, lies

---

[1] Department of Biology, San Diego State University, San Diego, California 92182-0057.

at an elevation of 1,036–1,060 m on the Shaniko Plateau, formed of Columbia River basalts, and includes several ravines that fall steeply northward into the valley of Ward Creek, 122 m below. The preserve has a cold, semidesert climate with an average annual precipitation of 280 mm. The surface of the plateau is mounded "biscuit scabland" with Mima mounds that range up to about 2 m in height and 20 m in diameter. The mound soils are classed as Condon eolian silt loams, and the intermound soils as Bakeoven residual very cobbly loams. The vegetation of mounds and deeper upland soils is dominated by Idaho fescue (*Festuca idahoensis*) and bluebunch wheatgrass (*Agropyron spicatum*). The shallow intermound soils are dominated by scabland sagebrush (*Artemisia rigida*), Sandberg bluegrass (*Poa scabrella*), several species of biscuitroot (*Lomatium* spp.), and bitterroot (*Lewisia rediviva*). The northern pocket gopher (*Thomomys talpoides*) is abundant throughout the preserve. A comprehensive physical and biotic inventory of the LMGP is given by Copeland (1980).

Relationships of mound and moundfield characteristics to slope and aspect were explored by sampling mounds throughout the LMGP and on a small area of adjacent ranch land. For this sampling, an aerial photo with a superimposed 100 × 100-m grid was used. Some grid units that included very steep slopes or canyon bottoms were largely or entirely unmounded. Since the objective of the study was to examine mound characteristics in relation to slope, only mounded grid units (> 50% of the surface showing mound-intermound topography) were considered for sampling. This criterion also assured that the grid units selected were internally uniform in their slope. These grid units, with the aid of a topographic map, were also grouped tentatively into five aspect classes: level (with an overall slope less than 2.5°), or north-, east-, south-, or west-facing. All grid units within the 153-ha LMGP were considered. In addition, to allow adequate representation of south-facing slopes, a 10-ha area of land north of Ward Creek was also included. Sets of 7 grid units were chosen by random coordinates in each of the five aspect classes (a total of 35 grid units).

The aerial photo was then used to locate these grid units (hereafter termed plots) in the field. The overall aspect of each plot was determined with a compass and the slope steepness measured with an inclinometer. A count of the mounds in each plot was obtained, and the mound nearest the plot center was designated for detailed measurements. Maximum mound height was measured with a meter stick and line level. The orientation of the long axis of the mound (downslope direction) was measured with a compass. Maximum and minimum diameters were measured with a meter tape, and the components of these diameters relative to the highest point on the mound were also recorded (mound top to upslope edge, top to downslope edge, etc.). Distances to the first and second nearest neighbors (between mound high points) were also measured with a meter tape, as was the minimum distance between the highest points of the two mounds that were furthest apart in this three-mound set. The fraction of the mound encircled by beds of bare, size-sorted stones (Cox and Allen 1987a) was recorded for the upslope and downslope halves of the mound. The length of stone beds diverging from that surrounding the mound and extending downslope ("tails") was recorded. The maximum length of this measurement was the point at which this "tail" reached another mound. Finally, the number of discrete pocket gopher activity areas was recorded as an estimate of the number of animals occupying the mound. Areas with surface heaps or plugged tunnel openings were considered separate activity areas when they were separated by more than 5 m.

From these measurements a number of descriptive characteristics were calculated. Mound area was calculated assuming that the base was a circle or ellipse, and volume was computed on the assumption that the mound was a segment of a sphere or prolate spheroid. Elongation (E1) was computed from the following relationship:

$$\mathrm{E1} = \sqrt{(a^2 - b^2)}/a$$

where *a* and *b* are the major and minor radii. A second measure of elongation (E2) was also calculated as the ratio of the major to minor diameters of the mound. Asymmetry (AS) was calculated

$$\mathrm{AS} = [(1 - Sl)^2 + (1 - Ss)^2]^{0.5}$$

where *Sl* and *Ss* are the asymmetries on the

TABLE 1. Characteristics of Mima mounds and moundfields on plots differing in slope steepness at the Lawrence Memorial Grassland Preserve, north central Oregon. Values are means ± standard errors.

Characteristic	Overall (n = 35)	Slope steepness (°) 0–2.5 (n = 6)	2.5–5.0 (n = 15)	5.0–7.5 (n = 8)	7.5–10.0 (n = 6)
Mound features					
Height (cm)	68.7 ± 2.8	81.7 ± 6.8	67.9 ± 4.4	62.9 ± 5.1	65.7 ± 6.5
Area (m^2)	145.9 ± 14.6	188.0 ± 25.1	174.9 ± 24.7	118.2 ± 26.2	68.0 ± 8.9
Volume (m^3)	52.8 ± 6.2	78.6 ± 13.7	60.6 ± 10.1	40.6 ± 11.2	23.5 ± 5.3
Elongation	1.42 ± 0.11	1.23 ± 0.18	1.46 ± 0.20	1.73 ± 0.20	1.07 ± 0.11
Asymmetry	0.59 ± 0.08	0.14 ± 0.04	0.59 ± 0.08	0.78 ± 0.23	0.77 ± 0.27
Sorted stone beds					
Upslope side (%)	36.6 ± 5.6	59.2 ± 17.1	35.3 ± 7.8	34.4 ± 13.1	20.0 ± 8.2
Downslope side (%)	25.8 ± 4.9	45.8 ± 16.6	28.0 ± 7.5	17.5 ± 7.0	11.7 ± 7.9
Overall (%)	31.5 ± 4.7	52.5 ± 15.6	31.7 ± 6.3	25.9 ± 9.5	17.5 ± 7.7
Downslope tails (m)	2.17 ± 0.64	0	1.65 ± 0.73	4.89 ± 2.13	2.02 ± 1.11
Moundfield features					
Density (ha^{-1})	21.6 ± 1.2	18.8 ± 2.3	21.5 ± 1.9	24.4 ± 3.1	21.2 ± 2.9
Connection	0.11 ± 0.03	0.05 ± 0.05	0.18 ± 0.06	0.04 ± 0.04	0.09 ± 0.06
Linearity	0.84 ± 0.02	0.74 ± 0.06	0.88 ± 0.03	0.77 ± 0.06	0.91 ± 0.03
Mounded surface (%)	31.5	35.3	37.6	28.8	14.4

long and short axes, respectively, calculated

$$Sl = a'/a \qquad Ss = b'/b$$

where a' and b' are the longer, and a and b the shorter distances from mound edge to peak along the major and minor axes. Connection (C) of the sampled mound to the two nearest mounds on opposite sides was calculated as the mean of ratios of heights of between-mound divides to maximum mound height. Linearity (L) of alignment of the sampled mound and its two nearest neighbors was determined as the ratio of the sum of distances measured from center to center for a series of mounds to the single straight-line distance between the first and last in the sequence.

Data on mound and moundfield characteristics were analyzed by BMDP statistical software procedures (Dixon 1983). Logarithmic and arc-sine transformations were employed to achieve normality for some variables. Means and standard errors were computed for plot data grouped by slope aspect and slope steepness classes, and these classes were then compared by t-tests and ANOVA (BMDP 1D and 7D). Correlations among all combinations of variables and stepwise linear regressions using selected variables as the dependent variable were also performed (BMDP 2R).

Plant names follow Hitchcock and Cronquist (1973).

RESULTS

Measurements of the overall slope aspect in the field revealed that several of the plots tentatively placed in particular aspect classes actually fell in other classes. As a result, the final set of samples comprised 10 N-facing, 5 E-facing, 5 S-facing, and 8 W-facing plots (Table 1).

Mound and moundfield characteristics showed a complex relationship to slope aspect and steepness. With respect to slope steepness, mounds at the LMGP were confined to slopes less than about 10° in steepness. Mounds exhibited greatest height, basal area, and volume on level areas or very gentle ($< 2.5°$) slopes (Table 1). Basal area and volume declined progressively with increased slope steepness (ANOVA, $F_{3,31} = 3.62$, $P < .05$ for area; $F = 3.29$, $P < .05$ for volume). The mean height of mounds on level to very gently sloping areas was significantly greater than on steep (5.0–7.5°) slopes ($t = 2.26$, $DF = 12$, $P < .05$). Volume, the best overall indicator of mound size, showed a strong negative correlation ($r = -.496$, $P < .01$) with slope steepness (Fig. 1).

Mound asymmetry and elongation were both greatest on steep (5.0–7.5°) slopes (Table 1). Asymmetry was significantly lower for mounds on level to very gently sloping

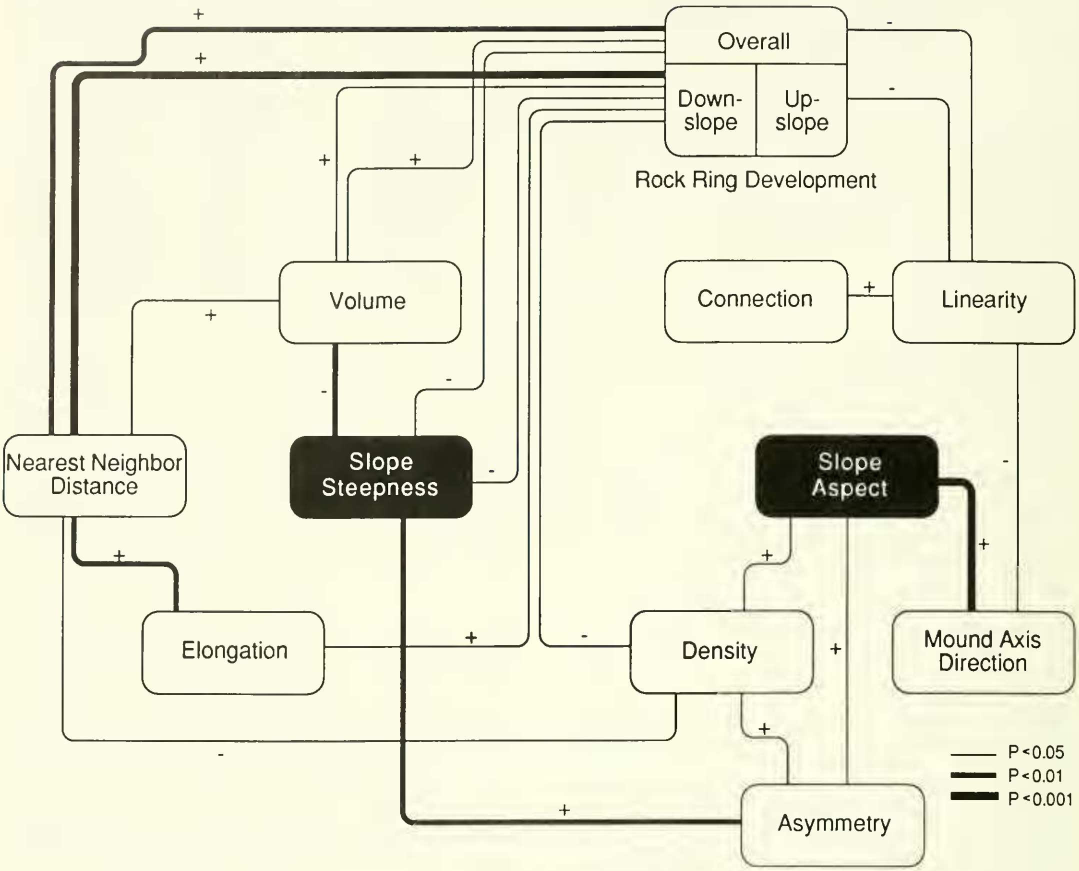

Fig. 1. Correlation relationships between major variables of mound and moundfield geometry for plots sampled on slopes of differing steepness and aspect at the Lawrence Memorial Grassland Preserve, north central Oregon, June 1987.

(0–2.5°) areas than on gentle (2.5–5.0°) slopes ($t = 3.30$, DF $= 19$, $P < .01$), steep slopes ($t = 2.35$, DF $= 12$, $P < .05$), or very steep (7.5–10.0°) slopes ($t = 2.33$, DF $= 10$, $P < .05$). Asymmetry was also strongly correlated ($r = .449$, $P < .01$) with slope steepness (Fig. 1). Elongation, defined as the ratio of long to short mound axis, was significantly greater on steep slopes than on level to very gently sloping areas ($t = 3.07$, DF $= 12$, $P < .01$). Elongation was significantly greater on steep than on very steep slopes ($t = 2.56$, DF $= 12$, $P < .05$).

The development of encircling beds of bare, size-sorted stones was strongest on level to very gently sloping plots (Table 1), the degree of overall development being negatively correlated ($r = -.343$, $P < .05$) with slope steepness (Fig. 1). The negative correlation between the development of sorted stone beds and slope steepness was stronger on the downslope side of mounds ($r = -.367$, $P < .05$) than on the upslope side ($r = -.304$, $P > .05$).

Moundfield characteristics showed weaker patterns. Density of mounds showed little variation with slope steepness (Table 1). Connection and linearity, which were positively correlated ($r = .343$, $P < .05$), exhibited highest values on steeper slopes. Linearity was significantly lower on level to very gently sloping (0–2.5°) plots than on plots with gentle (2.5–5.0°) slopes ($t = 2.29$, DF $= 19$, $P < .05$) or very steep (7.5–10.0°) slopes ($t = 2.28$, DF $= 10$, $P < .05$). The combination of mound size (basal area) and density resulted in a greater surface coverage by mounds on very
]

TABLE 2. Characteristics of Mima mounds and moundfields on plots differing in aspect at the Lawrence Memorial Grassland Preserve, north central Oregon. Values are means ± standard errors.

		Aspect				
Characteristic	Overall (n = 35)	Level (n = 7)	North (n = 10)	East (n = 5)	South (n = 5)	West (n = 8)
Mounds						
Height (cm)	68.7 ± 2.8	80.7 ± 5.8	75.6 ± 4.4	60.0 ± 8.0	54.2 ± 5.4	63.9 ± 5.2
Area (m^2)	145.9 ± 14.6	172.3 ± 26.4	146.6 ± 24.5	117.1 ± 42.3	121.0 ± 42.4	155.2 ± 39.2
Volume (m^3)	58.2 ± 6.2	71.5 ± 13.6	57.1 ± 11.1	40.7 ± 18.3	30.7 ± 8.4	52.1 ± 15.6
Elongation	1.42 ± 0.11	1.10 ± 0.20	1.32 ± 0.20	1.72 ± 0.32	1.60 ± 0.18	1.51 ± 0.28
Asymmetry	0.59 ± 0.08	0.15 ± 0.03	0.51 ± 0.08	1.00 ± 0.34	0.66 ± 0.30	0.75 ± 0.14
Rock circles						
Upslope side (%)	36.6 ± 5.6	50.7 ± 16.7	33.5 ± 11.5	41.0 ± 18.6	38.0 ± 10.7	24.4 ± 6.2
Downslope side (%)	25.8 ± 4.9	39.3 ± 15.4	20.5 ± 10.5	20.0 ± 10.5	25.0 ± 12.2	25.0 ± 11.3
Overall (%)	31.5 ± 4.7	45.0 ± 15.2	27.0 ± 9.1	30.5 ± 13.5	31.5 ± 10.3	25.9 ± 6.1
Rock tails (m)	2.17 ± 0.64	0	1.95 ± 1.06	4.64 ± 3.25	3.28 ± 1.63	2.11 ± 1.03
Moundfield features						
Density (ha^{-1})	21.6 ± 1.2	17.8 ± 2.2	20.0 ± 1.3	23.6 ± 4.1	26.8 ± 5.0	22.5 ± 2.6
Connection	0.11 ± 0.03	0.09 ± 0.06	0.20 ± 0.09	0.06 ± 0.06	0.08 ± 0.08	0.06 ± 0.04
Linearity	0.84 ± 0.02	0.78 ± 0.06	0.91 ± 0.03	0.75 ± 0.09	0.82 ± 0.04	0.86 ± 0.04
Mounded surface (%)	31.5	30.7	29.3	27.6	32.4	34.9

gentle to gentle slopes than on steep to very steep slopes.

Data for mounds grouped by slope aspect (Table 2) indicate that mound size (height, basal area, volume) was greatest on level plots and next greatest in height and volume on north-facing slopes. Mounds were smallest in both height and volume on south-facing slopes and next smallest on east-facing slopes. The variation among heights on plots differing in aspect was significant (ANOVA, $F_{4,30} = 3.48$, P < .05). Mean volume on south-facing slopes was significantly less than on level sites (t = 2.31, DF = 10, P < .05).

Mounds were least elongate or asymmetric on level and north-facing plots, and most elongate and asymmetric on east-facing slopes (Table 2). Elongation, expressed as the ratio of longer to shorter axis, was significantly greater for east- and south-facing plots than for level plots (t = 3.14 and 2.76, respectively, for east- and south-facing plots, DF = 10, P < .05). Variation in asymmetry was significant among aspect groups (ANOVA, $F_{4,30} = 3.29$, P < .05). Elongation of mounds was closely parallel to slope, the long axis of the mound being very highly correlated with the slope direction (Fig. 3, r = .822, P < .001). The development of sorted stone circles differed little for slopes of differing aspect (Table 2). Downslope tails of sorted stones were noted on slopes of all aspects.

Mound density was positively correlated with slope aspect, expressed as deviation in degrees from north (r = .405, P < .05). Density ranged from 17.8 mounds ha^{-1} on level plots to 26.8 mounds ha^{-1} on south-facing slopes (Table 2). Linearity of a sample mound and its two nearest neighbors was greatest for north-facing and least for east-facing slopes. Linearity was significantly greater for north-facing slopes than for level plots (t = 2.26, DF = 15, P < .05).

Several other important relationships were not directly linked to either slope steepness or slope aspect (Fig. 1). A number of these centered on nearest neighbor distance and stone circle development. Nearest neighbor distance was positively correlated with mound volume (r = .349, P < .05). In addition, nearest neighbor distance showed a strong, direct correlation with mound elongation (r = .449, P < .01) and stone circle development (r = .468, P < .01). Furthermore, the correlation of nearest neighbor distance to development of the stone circle on the downslope side of mounds was very strong (r = .641, P < .001). Mound volume also showed a direct relationship to stone circle development, both overall (r = .346, P < .05) and on the downslope side (r = .415, P < .05). The more elongate a mound, the greater was the development of the stone circle on its downslope side (r = .379, P < .05). The greater the density of mounds, however, the poorer was the development of the stone circle on the downslope side of the mound ($r = -.423$, $P < .05$). Linearity of mound arrangement, on the other hand, was negatively related to development of the stone circle, both overall ($r = -.339$, $P < .05$) and on the upslope side ($r = -.335$, $P < .05$). Finally, density showed a positive correlation with asymmetry ($r = .364$, $P < .05$), and mound axis direction was negatively correlated with linearity of mound arrangement ($r = -.335$, $P < .05$).

Discussion

The major patterns of variation of mound and moundfield characteristics with slope steepness and aspect are listed below.

1. Mounds show maximum size, circular and symmetrical form, low connection and linearity, and well-developed stone circles on level sites.
2. On slopes, mounds become smaller and more elongate and asymmetrical, with the long axis parallel to the slope, and show greater connection and linearity of arrangement.
3. On slopes, stone circles become weaker, especially on the downslope side of mounds, and stone beds diverge to form downslope tails.
4. Slope effects are, in general, more intense on south- and east-facing slopes than on north- and west-facing slopes (except for connection, which tends to peak on gentle north-facing slopes).

Much variation exists in the literature concerning the steepness of slopes on which mounds occur. Waters and Flagler's (1929) data on the Columbia Plateau and nearby areas record mounds on slopes up to only 6° in steepness, and Kaatz (1959) stated that mounds occur on slopes up to about 7° in steepness. Brown (1951), however, reported that mounds in this region occur on slopes up to 35–45°. Vitek (1973) reported mounds in southern Colorado on mountain slopes up to 20° in steepness, and in southern California, Cox (1984) found mounds on slopes up to 30° in steepness. Price (1949) stated that mounds occur in the western states in mountain meadows with slopes up to 20–30°. This variation in maximum steepness of mounded slopes may be real and may relate to soil texture and other factors affecting vulnerability to erosion. Mounds may occur only on slopes of 20° steepness or greater when soils are rich in clays, as they are in many locations in southern California (Cox 1984).

Researchers also offer diverse statements on how mound shape varies with slope steepness. Scheffer (1958) states that Mima mounds are "generally circular in shape as seen from above, regardless of slope." Vitek (1973), in southern Colorado, found that mounds tend to be nearly circular even on slopes up to 10.4° in steepness. On the Columbia Plateau, however, mounds are usually described as being more elongate on slopes. In southern Washington and northern Oregon, Waters and Flagler (1929) reported that the mean ratio of major to minor axes increases with increasing slope to a value of 1.43 on slopes of 6° steepness. The long axis of these mounds is said to be parallel to the slope. Malde (1964) noted that mounds in southwestern Idaho are typically circular, but that on hillsides they are noticeably elliptical, with the long axis directed downslope. Kaatz (1959), in central Washington, found that the typical mound is elliptical in shape, with a ratio of major to minor axis of about 1.41, the long axis being parallel to the slope. Olmsted (1963) found that mounds in eastern Washington are often elongate, the ratio of major to minor axis being 1.1–1.5. He also stated that the long axis is aligned with prevailing winds and is sometimes across slopes rather than parallel to them. Fosberg (1965) stated that in Twin Falls County, Idaho, mounds elongate into downslope stripes.

A degree of connection, or confluence, of mounds and their alignment into rows parallel to the slope has been noted by several workers. Waters and Flagler (1929), Malde (1964), and Fosberg (1965) describe mounds on the Columbia Plateau as forming beadlike rows along small drainage divides or between stone stripes on steeper slopes. Perhaps the best overall description of this pattern, together with that of mound form, is given by Brown (1951) for sites near Maupin, Oregon:

> On the steeper slopes they are oriented in more or less parallel lines along the rill divides, tend to be elongate and coalesce and are not as high nor as perfectly kept up as on the level. Looking at these slopes from a distance

> or studying aerial photos, one gains the impression of a continuous mound down the slope as though it constituted the entire rill divide. A close inspection, however, reveals that the crest of the strip is not even, that it is divided by well formed mounds rising above the level of the surrounding soil.

Fewer authors describe changes in the arrangement of sorted stone beds as slope steepness increases. Malde (1961, 1964) states that in southwestern Idaho the stone pavements surrounding mounds change progressively to parallel stone stripes running up- and downslope, implying the disappearance of pavement sections on the up- and downslope edges of mounds. Kaatz (1959), stating that stone circles and networks change to sorted stone stripes on steep slopes, also notes that sorted stripes may occur without any upslope connection to the former features. Brunnschweiler (1962) describes a similar pattern and diagrams a configuration in which stone "tails" arise from stone rings encircling mounds, or from intermound polygonal networks, to extend downslope. Pyrch (1973) noted that sorted stone stripes occur on slopes up to a maximum steepness of 15–33°. At the LMGP, Cox and Allen (1987a) found that on level areas the development of stone circles is directly correlated with mound size, and that on slopes the initial pattern of modification is the weakening of the bordering bed on the downslope side of the mound and the divergence of downslope "tails."

Are these mound features compatible with the basic hypothesis of origin of both mounds and associated stone circles, polygonal nets, and stripes by the soil translocation activities of pocket gophers? And if so, how does this mechanism interact with site characteristics related to steepness and aspect to yield the observed patterns?

Let us first consider the implications of the relationship of the intensity of moundward soil translocation by pocket gophers to distance from the center of a small mound and elevation below its top, as observed by Cox and Allen (1987b). For a mound on a level site, average moundward translocation increased with distance from the mound center, and average upward translocation increased with elevation below the mound top. On a level site these tendencies would be distributed symmetrically, other factors being equal, and the mound would tend to enlarge symmetrically, maintaining a circular shape.

For a similar small mound on a slope, however, differences in translocation would result even if the amount of tunneling activity remained the same in terms of distance and direction from the mound center. On the sides of the mound lying on the slope contour, moundward and upward translocation will be similar to soil movements on a mound on level ground. On the downslope side of the mound, however, an animal must move soil a greater vertical distance to achieve the same horizontal displacement. Since this requires greater energy expenditure, horizontal displacement will probably often be less than expected. On the upslope side of the mound, in contrast, a given horizontal displacement will occur with less vertical displacement. In some cases, of course, much of the actual horizontal displacement will be downslope. Thus, expenditure of the same energy will lead to a greater than expected horizontal displacement.

The consequence of differences in mean displacement distance is that more soil will be translocated onto the upslope side of the mound than onto the downslope or lateral sides. The mound should thus grow most in a lateral and upslope fashion. However, this growth could permit a circular form to be retained as long as the average of upslope and downslope addition rates equals the addition rates to the lateral edges of the mound. Such a pattern will prevail whenever the mean horizontal translocation distance of soil at a given distance from the mound center is linearly related to the mean slope of the translocation path (Fig. 2).

If the relationship of mean displacement distance to slope is curvilinear and convex, however, then additions to the lateral edges will be greater than expected, and to the upslope and downslope edges less than expected; thus, the mound will expand in width (across the slope). If the relationship is curvilinear and concave, additions to the upslope and downslope edges will be greater than expected, and those to the lateral edges less than expected; the mound will elongate up- and downslope. In the latter case, the total amount of soil translocated onto the downslope side of the mound will still be much less than that moved onto the upslope surface. As the mound grows in height, addition to the downslope side of the mound will also decline. At the same time, slope conditions on

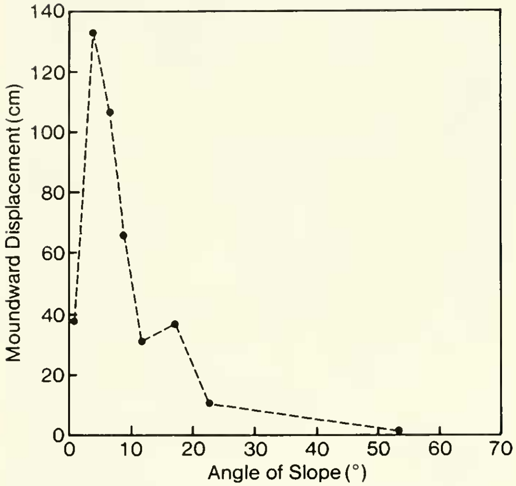

Fig. 2. Horizontal displacement distance (moundward) for soil mined by *Thomomys bottae* in southern California in relation to slope for data from Cox and Allen (1987b).

the upslope side of the mound will still permit heavy translocation onto the mound surface. Thus, slope relationships should cause erosional loss of soil to balance moundward translocation sooner on the downslope side of the mound than on the upslope side. Upslope growth should therefore continue after downslope growth has stopped.

Data from soil translocation studies of *Thomomys bottae* in southern California (Cox and Allen 1987b) suggest that soil translocation by pocket gophers of this genus varies with steepness in a curvilinear, concave fashion over a range from less than 5° to more than 50° (Fig. 3). These data were obtained in studies of soil translocation on level sites, where the only slope was that of the mounds themselves.

Elongation of mounds on the Columbia Plateau should be coupled with an upslope movement of the mound high point. At maximum size, the highest point of an elongated mound should thus be nearest its upslope end.

Elongation of mounds should lead to connection with adjacent mounds up- and downslope when the soil mantle is deep enough to permit the development of large mounds. Such connection may create a linear, "beaded" arrangement of mounds parallel to the slope. This arrangement will give a strong measure of linearity if the two nearest neighbors of a given mound are upslope and downslope in the connected line. Strong linearity of arrangement on a slope would thus imply that the mean distance between mounds in the same line is less than that between mounds in different lines. This should not be the case if uniformly spaced mounds develop on a slope and those directly up- and downslope from each other become connected. Our data show only a weak relationship between slope steepness and linearity, suggesting that little more than the connection of mounds lying up- and downslope from each other has occurred.

The presence of a mound on a slope would modify the flow of water across the slope, concentrating it along the upper and lateral sides of the mound and producing a dry shadow downslope (Cox and Allen 1987a). The concentrated flow of water along the sides of a mound would tend to continue directly downslope. These areas of maximum wetness favor the formation of sorted stone beds extending downslope. Several possible mechanisms may contribute to the transformation of beds encircling the mounds into elongate stripes paralleling them. Growth of fleshy-rooted plants may lead to extensive tunneling by pocket gophers in these areas. The collapse of deep tunnels and the downward settling of soil and small stones during the wet season may thus sort and expose stones near the surface (Cox and Allen 1987a). Erosion may also play an important role, particularly as slope steepness increases.

Figure 4 diagrams a hypothesis of how circular, isolated mounds surrounded by sorted stone nets become transformed into elongate, interconnected mounds bordered by linear beds of sorted stones. This hypothesis predicts that lines of mounds on slopes should be separated by two stone stripes, one representing the fusion of downslope extensions of the encircling beds of each line of mounds. Examination of aerial photos of sloping areas on the LMGP shows that this is generally true. These observations strongly support the overall hypothesis that pocket gophers interact with physical conditions and processes to produce the distinctive patterns of mounds and sorted stone beds on the Columbia Plateau.

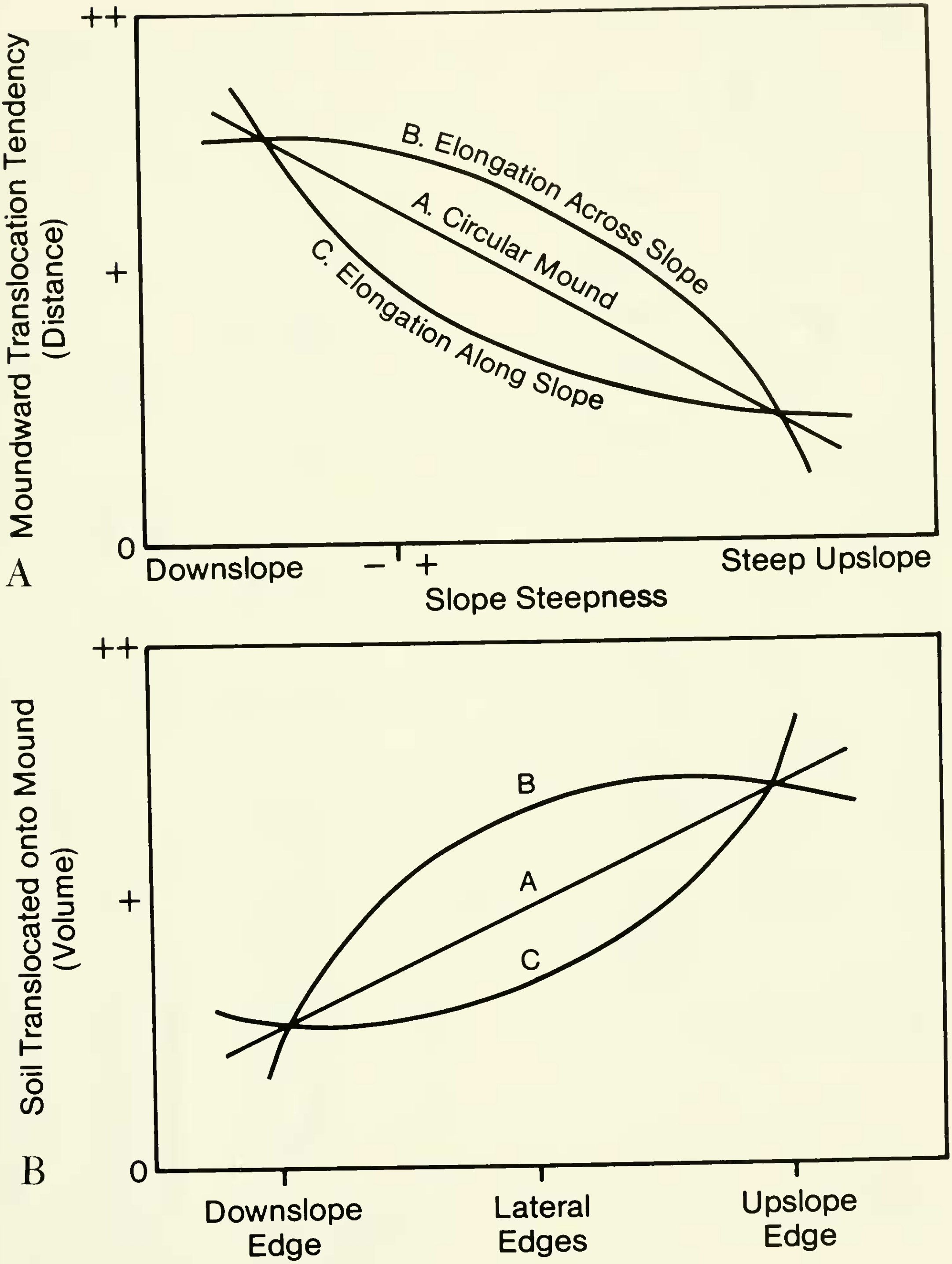

Fig. 3. (A) Possible relationships between mean horizontal translocation distance (moundward) and slope steepness. (B) Volume of soil moved onto mound surface at various points around mound perimeter by pocket gopher translocation in relation to slope steepness, based on the relationships outlined in (A) for a mound of a given slope.

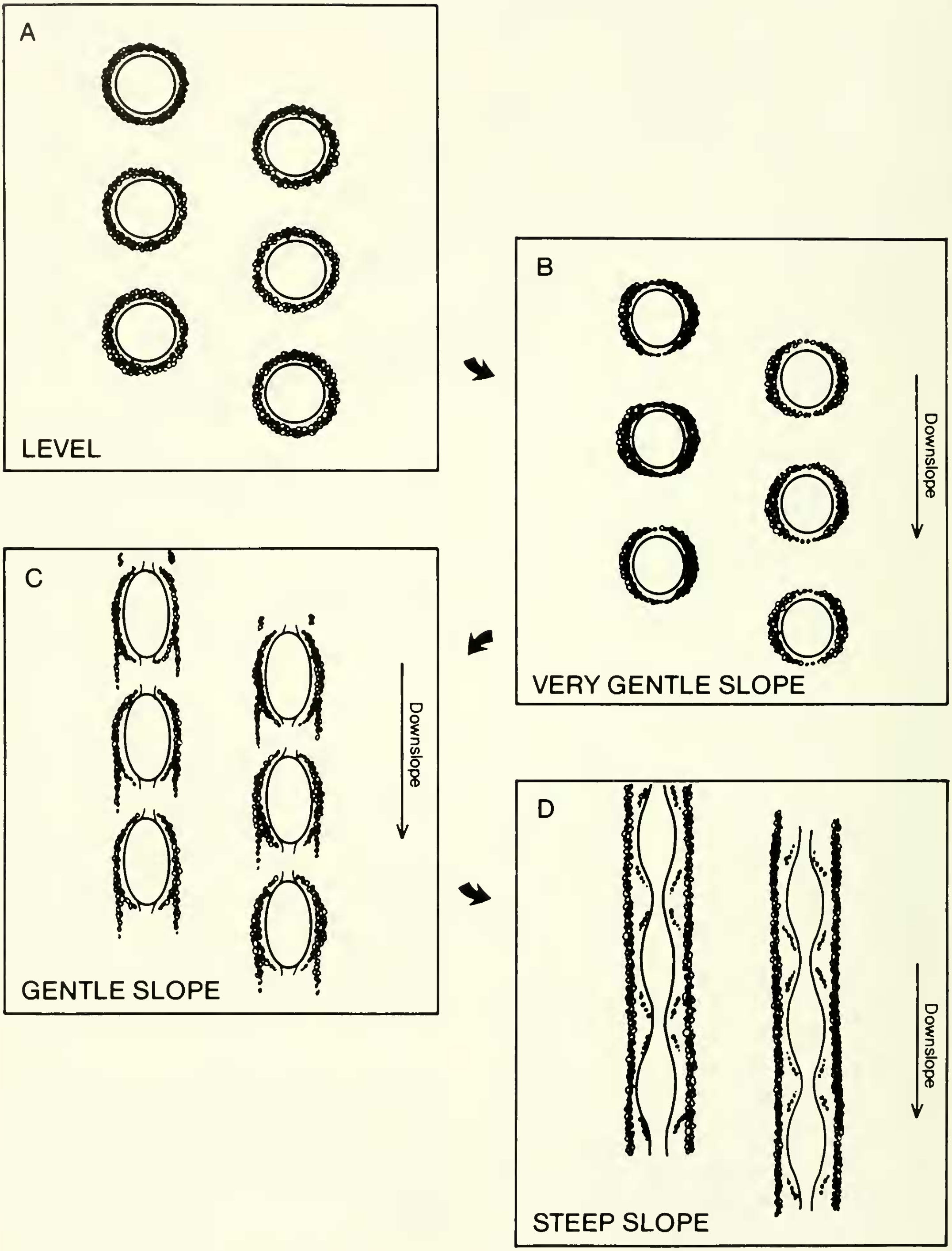

Fig. 4. Diagrammatic model of the transition of unconnected, circular mounds with encircling stone rings on level sites to linearly connected, elongate mounds bordered by stone stripes on steep slopes.

ACKNOWLEDGMENTS

I thank Elizabeth Lucas for assistance in field studies and in laboratory analyses of mound and moundfield geometry and Annan Priday for permission to conduct much of the work on areas of the Priday Brothers Ranch adjacent to the LMGP. Donald B. Lawrence gave advice and encouragement throughout the study. J. Hunt, J. R. Mackay, and V. B. Scheffer provided valuable comments on an earlier draft of the manuscript. This study was carried out under a contract with the Oregon Chapter of the Nature Conservancy and was supported in part by grant INT-8420336 from the U.S. National Science Foundation.

LITERATURE CITED

BROWN, H. C. 1951. Mound microrelief of the Columbia Plateau and adjacent areas. Unpublished manuscript. 36 pp.

BRUNNSCHWEILER, D. 1962. The periglacial realm in North America during the Wisconsin glaciation. Biuletyn Peryglacjalny 11: 15–27.

COPELAND, W. N. 1980. The Lawrence Memorial Grassland Preserve: a biophysical inventory with management recommendations. Unpublished report (revised 1983), Oregon Chapter, Nature Conservancy, Portland.

COX, G. W. 1984. The distribution and origin of Mima mound grasslands in San Diego County, California. Ecology 65: 1397–1405.

COX, G. W., AND D. W. ALLEN. 1987a. Sorted stone nets and circles of the Columbia Plateau: a hypothesis. Northwest Science 61: 179–185.

———. 1987b. Soil translocation by pocket gophers in a Mima moundfield. Oecologia 72: 207–210.

COX, G. W., AND C. G. GAKAHU. 1986. A latitudinal test of the fossorial rodent hypothesis of Mima mound origin in western North America. Zeitschrift für Geomorphologie 30: 485–501.

COX, G. W., C. G. GAKAHU, AND D. W. ALLEN. 1987. The small stone content of Mima mounds in the Columbia Plateau and Rocky Mountain regions: implications for mound origin. Great Basin Naturalist 47: 609–619.

DALQUEST, W. W., AND V. B. SCHEFFER. 1942. The origin of the Mima mounds of western Washington. Journal of Geology 50: 68–84.

DIXON, W. J. 1983. BMDP statistical software. University of California Press, Berkeley.

FOSBERG, M. A. 1965. Characteristics and genesis of patterned ground in Wisconsin time in a chestnut soil in southern Idaho. Soil Science 99: 30–37.

HITCHCOCK, C. L., AND A. CRONQUIST. 1973. Flora of the Pacific Northwest. University of Washington Press, Seattle.

KAATZ, M. R. 1959. Patterned ground in central Washington: a preliminary report. Northwest Science 33: 145–156.

MALDE, H. E. 1961. Patterned ground of possible solifluction origin at low altitude in the western Snake River Plain, Idaho. United States Geological Survey Professional Paper 424-B, 170–173.

———. 1964. Patterned ground on the western Snake River Plain, Idaho, and its possible cold-climate origin. Geological Society of America Bulletin 75: 191–207.

OLMSTED, R. K. 1963. Silt mounds of Missoula flood surfaces. Geological Society of America Bulletin 74: 47–54.

PRICE, W. A. 1949. Pocket gophers as architects of Mima (pimple) mounds of the western United States. Texas Journal of Science 1: 1–17.

PYRCH, J. B. 1973. The characteristics and genesis of stone stripes in north central Oregon. Unpublished thesis, Portland State University, Portland, Oregon.

SCHEFFER, V. B. 1947. The mystery of the Mima mounds. Scientific Monthly 65: 283–294.

———. 1958. Do fossorial rodents originate Mima-type microrelief? American Midland Naturalist 59: 505–510.

VITEK, J. D. 1973. The mounds of south-central Colorado: an investigation of geographic and geomorphic characteristics. Unpublished dissertation, Oklahoma State University, Stillwater.

WATERS, A. C., AND C. W. FLAGLER. 1929. Origin of small mounds on the Columbia River Plateau. American Journal of Science 18: 209–224.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

Received 10 June 1989
Accepted 30 November 1989